A COMBINED ACOUSTIC AND VISUAL SURVEY OF HUMPBACK WHALES OFF SOUTHEAST QUEENSLAND

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During their migrations between low latitude breeding areas and high latitude feeding areas, male humpback whales, *Megaptera novaeangliae*, are frequently heard singing, often continuously for many hours, and the sounds are audible for tens of kilometres. The stock that passes close to the coast of southeast Queensland has been extensively surveyed visually, but little is known of movements of whales that pass out of sight of land here, or in other areas of the world, where the migratory paths of humpback whales are often across open ocean. Acoustic surveying may be useful in quantifying whale movements in oceanic waters beyond the range of land surveying and an addition to visual monitoring. For acoustic surveys to be of use, the acoustic cues of the whales must be quantified and calibrated against the numbers of whales in an area. In 1997 we performed a combined visual and acoustic survey of whales migrating close to shore on the coast of southeast Queensland. Song activity was measured using two indices: number of passing singers and number of singer-hours observed within a 10km sector, and correlated with the number of whales passing through the area determined visually. Both were significantly correlated with r = 0.68 and 0.64 for singers and singer-hours respectively on a daily basis, and 0.79 and 0.89 respectively on a weekly basis. Linear regressions of daily measures of song activity with numbers of whales seen lead to estimates of ratios of singers with whales seen of 0.127 ± 0.027 (95% confidence interval) and singer-hours with whales seen of 0.288 ± 0.065. We discuss the possible use of these indices for conducting stand-alone acoustic surveys. ❐

Humpback whale, acoustic, song, migration, Australia.

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Traditionally, surveys of whales have been conducted using visual detection from elevated points along coastlines or from ships or aircraft. Visual surveys are limited primarily by the cryptic nature of cetaceans which spend much of their time underwater and are available for sampling only for the short proportion of time spent at the surface. They are also limited in their range of detection (particularly for ship-based surveys), are highly weather dependent and are restricted to daylight hours.

Many species of whales produce intense sounds that are audible to substantial distances and thus may be useful in surveying, especially in conditions where visual methods have limited effectiveness. Acoustic surveys have potential advantages over visual surveys: large cetaceans in particular may be detectable at many times the range possible with visual observations; detection is less dependent on weather; no restriction to daylight hours; and can be automated to varying extents (e.g. Thomas et al., 1986; Cummings & Holliday, 1985; Clark et al., 1986; Gillespie, 1997; Clark & Fristrup, 1997; Norris et al., 1999). While visual observations are limited to the small proportion of time that whales are at the surface in the field of vision, acoustic detection can be omnidirectional and possible for as long as the whales are vocalising. Deployment of automated acoustic recording systems that record for long periods (to be analysed after recovery) may be less expensive than ship-board surveys since they would require less ship time, and especially if analysis was automated. They are also non-intrusive and minimise sampling bias.

Acoustic surveying also has its limitations, the greatest being that it is indirect, i.e. counting cues rather than whales, and so requires careful calibration of the relationship between the occurrence of sounds and the numbers of whales (Buckland et al., 1993). It is effective only for species that vocalise regularly and, of those, only a portion of individuals in a stock may vocalise at any time. Also variations in background noise levels and local sound propagation characteristics cause significant variation in the distances of detection of vocalising whales.

Determining the spatial concentration of sources from the sounds detected, necessary in any estimate of abundance, is difficult without fixing the source positions. This usually requires three or more well spaced receivers with accurately known positions (e.g. Watkins & Schevill, 1972; Cummings & Holliday, 1985). This significantly increases cost, complexity of the work at sea and the amount of analysis required. Under certain circumstances, simpler methods are effective in determining the distances of the sources which can be related to source concentration (Cato, 1998).

Despite the potential of acoustics, few attempts have been made to calibrate acoustic cues against visual counts, particularly for mysticetes. The most extensive acoustic-visual surveys have been of bowhead whales (*Balaena mysticetus*) during their annual migration off Point Barrow, Alaska (Cummings & Holliday, 1985; Clark et al., 1986, 1996; Clark & Ellison, 1989, 2000; Raftery et al., 1990; Würsig & Clark, 1993; Zeh et al., 1993; Raftery & Zeh, 1998). Difficult weather conditions and the use of ice as a survey platform often severely restricted visual surveys of these whales. Arrays of fixed hydrophones have been used to track vocalising bowheads concurrently with visual observations, and mark-recapture and other statistical techniques have been applied to both data sets in an attempt to obtain more accurate population estimates (Gentleman & Zeh, 1987; Raftery et al., 1990; Zeh et al., 1993). Clark & Fristrup (1997) used a different approach to compare and calibrate acoustic and visual detection rates for blue whales (*Balaenoptera musculus*) and fin whales (*B. physalus*) during ship-based line transect visual and acoustic surveys combined with static hydrophone arrays. A statistical combination of acoustic and visual data attempted to improve density estimates (Fristrup & Clark, 1997). McDonald & Fox (1999) used an acoustic-only approach with a single bottom-mounted hydrophone to estimate minimum densities of fin whales off Hawaii.

Common to all these acoustic surveys has been the use of acoustics either to gather additional information to support limited visual surveys where the probability of visual detection is low or has not been previously determined, or as an almost entirely uncalibrated survey tool.

Humpback whales offer an opportunity to develop acoustic monitoring techniques using populations that can be well surveyed visually. Like many species of baleen whales, they undertake annual migrations from high latitude feeding areas to low latitude breeding areas. Humpback whales are often distributed along coastlines during part of this annual cycle, particularly on their breeding grounds which tend to be in shallow tropical waters (Dawbin, 1966) making them relatively accessible for surveying.

Many techniques have been used for visual surveys of these whales including aerial surveys (Herman & Antinoja, 1977; Bryden, 1985; Bannister, 1985; Bannister et al., 1991; Corkeron et al., 1994), ship-based surveys (Chittleborough, 1965; Herman & Antinoja, 1977; Whitehead, 1982; Stone & Hamner, 1988; Mattila & Clapham, 1989; Mattila et al., 1994), mark-recapture surveys using photographic identification of individuals (Whitehead, 1982; Baker et al., 1985; Darling & Morowitz, 1986; Baker & Herman, 1987; Flórez-González, 1991; Darling & Mori, 1993; Smith et al., 1999), and direct land-based counts of whales along migratory corridors (Bryden, 1985; Paterson & Paterson, 1989; Bryden et al., 1990, 1996; Paterson et al., 1994, 2001; Findlay & Best, 1996b). These surveys have been used to estimate absolute population levels, relative abundance and population growth rates, or population densities for specific areas.

Humpback whale vocalisations are also comparatively well studied. Male humpback whales produce long, complex vocalisations on the breeding grounds and during migration (Kibblewhite et al., 1967; Payne & McVay, 1971; Winn & Winn, 1978; Cato, 1984, 1991). These songs may be produced continuously for many hours at relatively high source levels. The combination of coastal distribution and reliable and distinctive vocalisation make humpback whales an ideal model for the development of acoustic surveying techniques.

Previous acoustic surveys of humpback whales have been conducted. Winn et al. (1975) performed ship-based visual and acoustic surveys on humpback whales in the West Indies to determine a population total for the breeding area, while Levenson & Leapley (1978) used a different technique to survey the West Indies, dropping sonobuoys from the air. Both studies made assumptions concerning the maximum detectable range of singing humpback whales

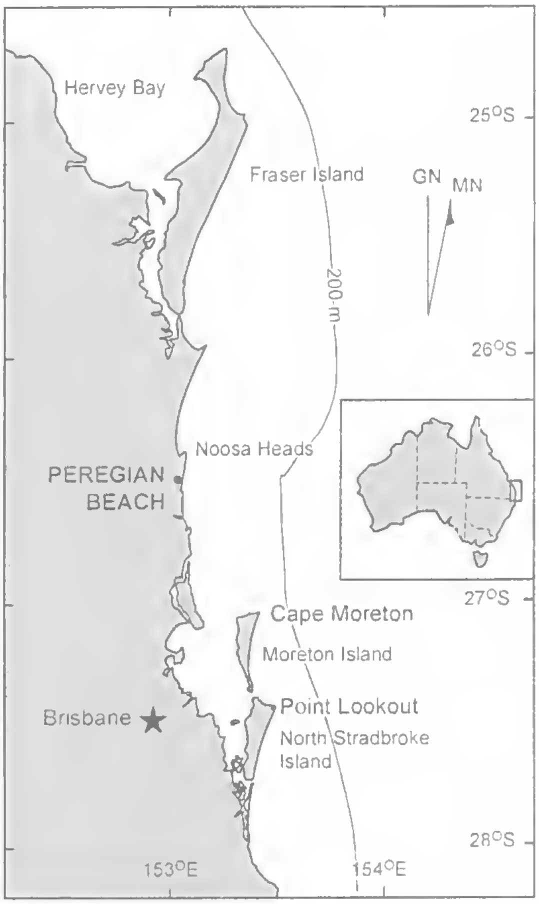

FIG. 1. Southeast Queensland showing study site of Peregian Beach and its westward location from other study sites of Point Lookout and Cape Moreton.

(12.8 and 9.3km respectively) without apparently determining local propagation characteristics and with only limited data available concerning source levels of song. Although Winn et al. attempted to develop a ratio of 'callers' to 'non-callers' based on 11 visual sightings, ratios varied widely for different areas leading to the conclusion that this ratio 'represents the greatest weakness in the acoustic method'.

Several subsequent acoustic surveys of humpback whales have simply relied upon the presence or absence of song to determine the migratory paths or distribution of whales (Clapham & Mattila, 1990; Dawbin & Gill, 1991; Gill et al., 1995; Norris et al., 1999). Frankel et al. (1995) used an array of hydrophones to determine the density of singers off Hawaii but did not attempt to relate it to the numbers of whales seen. Au et al. (2000) used remote recording techniques to show variations in singing activity across the winter and diurnally in Hawaii, but did not attempt to relate measurements of acoustic activity with singer density or abundance. They did, however, suggest that such stand-alone acoustic techniques could be used to provide either relative abundance estimates of humpback whales, or, if ground-truthed with visual and acoustic-positional surveys, absolute abundance estimates.

Land-based visual surveys along the migratory corridor on the east coast of Australia have been conducted regularly since 1978, mainly from Point Lookout on North Stradbroke Island with some from nearby Cape Moreton on Moreton Island (Fig.1), by two independent survey groups (Paterson, 1984; Paterson & Paterson, 1984, 1989; Paterson et al., 1994, 2001; and Bryden, 1985; Bryden & Slade, 1988; Bryden et al., 1990, 1996). Despite some differences in survey design and statistical methodologies, the two surveys are in broad agreement regarding both absolute and relative abundance, for example, Paterson et al. (1994) and Bryden et al. (1996) reporting populations of 1900 for 1992 and 1807 for 1993 respectively, with annual population growth rate estimates of 11.7% and 12.3% respectively. Humpback whales have also been shown to sing reliably in this area during migration (Cato, 1984, 1991; Noad et al., 2000; Macknight et al., 2001).

In this study, visual and acoustic surveys were performed simultaneously on this well described and surveyed migratory population of humpback whales off southeast Queensland to examine the possible use of acoustic stand-alone surveys for surveying humpback whale populations. Correlations between the number of whales visible and those singing are determined, and ratios of whales to measurable indices of acoustic activity are developed for future use in acoustic surveys.

MATERIALS AND METHODS

Visual and acoustic observations were conducted at Peregian Beach (26°30'S, 153°07'E) on the southern coast of Queensland (Fig. 1). The coast here comprises a long, straight, gently shoaling, sandy beach, the nearest headland 6km to the south. Data were collected during the southward migration of the whales in 1997, between 28 August and 31 October.

VISUAL DATA COLLECTION. Visual observations were made from the 73m high peak of a nearby hill, Emu Mountain, set 700m back from the beach. The view was unobstructed in all directions, coastal features allowing a 145° view of the ocean to the horizon (~30km). Two teams of 3-5 volunteers made observations in four shifts from 7am to 5pm daily. Position, composition and behaviour of whale groups were recorded. A theodolite was used to measure horizontal and vertical angles to whale pods with measurements calibrated by comparison of theodolite-tracked boat positions with GPS positions determined in the boat at the same time. At ranges of up to 10km the accuracy was determined to be within the differential error of the GPS and so was taken to be within 100m.

Data were also collected regarding environmental factors that might affect visibility or sightability including wind speed and direction, sea-state, cloud cover, glare, precipitation and air clarity. The number, type and positions of ships and boats were also recorded. Observations were abandoned in conditions of poor visibility or sightability including heavy or steady rain, and sea-state >4.

Data were entered into a spreadsheet daily (Excel, Microsoft) which calculated the positions of pods using the theodolite measurements. These calculations included the measured height of the theodolite above the peak of the hill, the tide height and a refraction coefficient ($k = 0.08$, see Appendix). Pod identities and continuity of sightings determined by the observers were checked against measured positions for consistency.

Aerial surveys out to 60km from shore in good visibility by Bryden (1985) indicated that <5% of humpback whales passed beyond 10km of the headlands of North Stradbroke and Moreton Islands, where most visual surveys have been conducted. He considered that 10km was the useful limit of visibility from shore under good conditions. Peregian Beach is ~100km north of Point Lookout (on Stradbroke I.) and ~45km west (Fig. 1). While we saw many whales at ranges far greater than 10km, we have limited this analysis to whales seen within 10km of shore. The closest approach of whales was only a few hundred metres offshore and so our observation area was considered to extend from shore to 10km seaward, and limited north and south between bearings 10° and 160° on the study grid (Fig. 2). The visual survey area was not centred on Emu Mt as it was inland from the coast and so would have included a significant area not available to migrating whales, and would have been less directly comparable with the acoustic survey area. Whales were seen travelling both northwards and southwards although some whale groups did not have enough sightings to determine direction of movement. These were assigned a direction according to the ratio of north-south whales observed during that day.

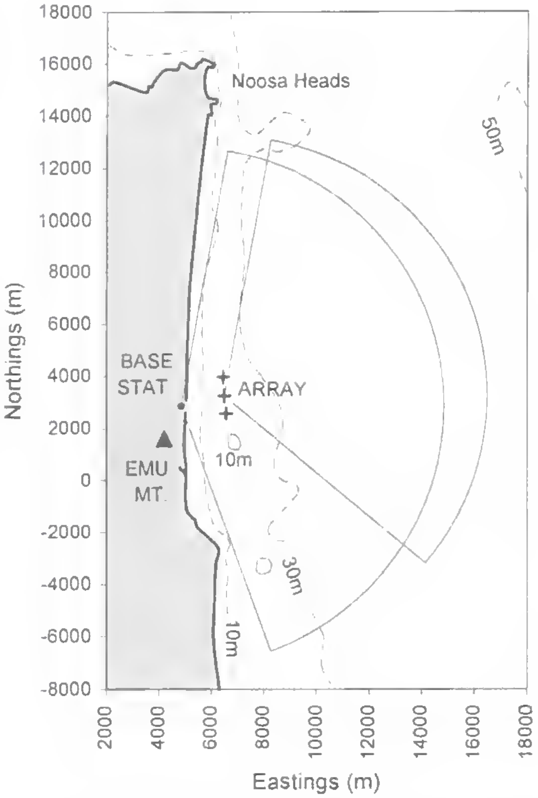

FIG. 2. Peregian Beach study site showing observation areas and grid system used (grid north lies between true and magnetic north). Visual observations were made from 73m high Emu Mt while acoustic recordings were made using three offshore hydrophones (crosses). The small shoal south of the array caused sudden and profound attenuation of song sounds of singers in the southern portion of the study area.

ACOUSTIC DATA COLLECTION. An array of three custom-designed hydrophone-buoys (A, B and C) was deployed 1,500m offshore in 20m of water (Figs 2,3). The hydrophone-buoys were spaced in a line ~750m apart, giving an array base-line of ~1,500m, with the central buoy B slightly offset to the west. Each buoy was moored by a 40kg concrete and steel clump attached to 6m of chain and a 4.5kg plough anchor. The body of each buoy was a hollow tube of PVC pipe supported by a fibreglass foam-filled 'torus' float. Each contained a sonobuoy VHF transmitter

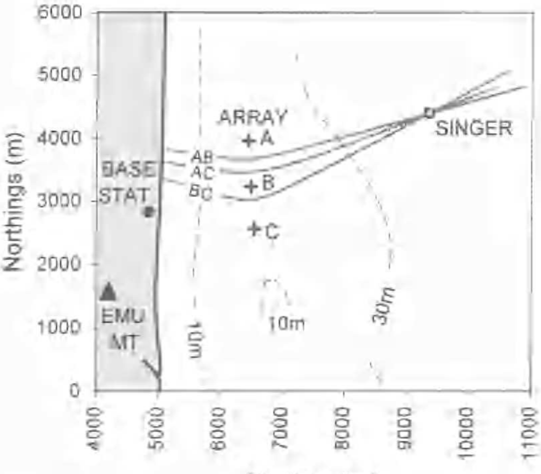

FIG. 3. Acoustic positioning of a singing humpback whale. Differences in the arrival time of sounds from the singer to each of the hydrophones were used to generate a hyperbola (grey line) for each pair of buoys. The point of intersection of the three hyperbolae (from buoy-pairs AB, BC and AC) was taken as the position of the singer. A small discrepancy in intersections resulted in a triangle, in which case the singer was taken to be at the centre.

(Spartan Electronics AN/SSQ – 41B) and a rechargeable battery pack (12V, 30A-h) and were designed to follow the rise and fall of the sea surface and remain upright, thus optimising the orientation of the transmitter antenna. This was achieved by attaching the mooring line at a point in relationship to the distribution of mass that minimised rotation in the vertical plane. A 40dB gain pre-amplifier (custom-built) was contained in a separate underwater housing attached to the mooring clump and connected to the buoy by standard RG58 coaxial cable (single core, 50Ohm) running along the anchor rope. A GEC-Marconi SH101X hydrophone was connected to the preamplifier by 10m of RG58 cable and was suspended from a small float attached to the anchor, approximately 1m above the substrate. The hydrophone cable was wound with string to help prevent low frequency vortex-shedding noise in conditions of significant current or groundswell.

Signals from the buoys were received by a Yagi antenna mounted as high as possible (~10m above sea-level) at the base station located 80m behind the beach. The antenna was connected to a four channel, low noise, VHF receiver. Signals from the receiver were split and passed to two desktop computers (IBM PC clones) – one for real-time spectrographic monitoring and the other for computation of singer positions – a four-track analog tape recorder (Tascam 424 Portastudio) and a stereo DAT recorder (Sony TCD-D7 Walkman). The audio signal was monitored continuously during the hours of visual observations. When a singer was detected with a signal-to-noise ratio sufficient to allow the pattern of the song to be determined, recording was initiated. Some tracking of singers occurred in real-time in the field while the majority occurred at a later time using the multi-track recordings.

Appropriate sounds in the song (rapidly frequency-modulating tonal sounds) were manually selected and sampled into the computer using Cool Edit 96 (Syntrillium). Matlab (Mathworks) customised software performed waveform cross-correlations of the same sound received on each of the three pairs of hydrophones (buoy-pairs AB, BC and CA) to determine the time-of-arrival-differences (TOADs) for each pair of buoys. Each of the three resulting TOADs was used to generate a hyperbola along which the source of the sound could lie. The intersection of the three hyperbolae was taken as the position of the singer (Fig. 3). While there is ambiguity inherent in this method (since the hyperbolae intersect at two points, one each side of the line of hydrophones), in our experiment the westerly solution was usually inland and could be discarded. Sequential calculation of positions allowed the singer to be tracked (Fig. 4).

Calibration and Ranging Error. The array was ground-truthed using two methods. The first was comparison of acoustically calculated positions with theodolite positions of visually identified singers (based on the timing of surface intervals predicted acoustically by features of the song) (Fig. 4). The second was experimental and involved the implosion of light bulbs under the research vessel at various locations in the study area. These bulbs, smashed at depth, produced a single brief popping sound audible at several kilometres range that could be acoustically positioned for comparison with GPS positions. Bulbs were enclosed in a fine net so that broken debris could be recovered.

As three hydrophones were necessary to calculate the location of the singer, acoustic tracking was not possible if one or more of the buoys was not operating. Time lost due to technical problems was minimal although the

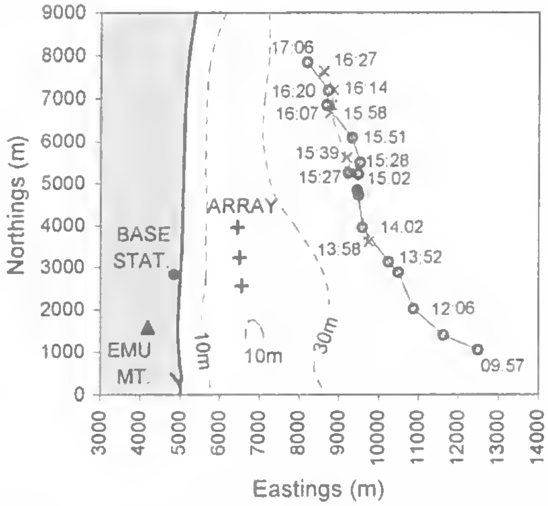

FIG. 4. An example of a combined visual and acoustic track of a singing humpback whale (70904s1) including times of locations. Acoustic positions are black circles and theodolite-generated visual positions are grey crosses.

buoys were removed from the water in the middle of the survey period for scheduled maintenance.

Quantification of Singing Activity. Although some singers passed very close to the array, only one singer went inside the array and then by only a few tens of metres. The area used for the acoustic survey was therefore taken as being a 10km sector out to sea from the array between the bearings 10° and 130° (Fig. 2) where the acoustic tracking was found to give reliable results. Although this did not correspond exactly to the 10km sector from the beach used for the visual survey, the two sectors overlapped substantially and could be considered to provide comparable visual and acoustic samples of the migrating whales.

Within this sector, the signal-to noise ratio (SNR) of the sounds used in the cross-correlation analysis was more than adequate for the purpose. The SNR of 'modulated bellows', the sound most frequently used, were calculated for 20 singers at 92 points within 13km of the array by measuring the relative levels of the signal and the background noise in the 1/3 octave band containing the centre frequency of the signal (210-400Hz), averaged over the duration of the sound (approx. 1.2sec). The mean SNR at a range of 10km was 22dB under average observational conditions.

Only song recorded during hours of visual survey were included in this analysis. As most visual observations were curtailed due to high sea-state and rain, and similar conditions also reduced singer detectability due to increased ambient noise, this ensured that visual and acoustic observations were directly comparable under favourable detection conditions.

Two methods of quantifying singing activity were used: 'number of singers' which was a count of the number of individual singers passing through the sector per 10 hours, and 'singer-hour index' which was determined by counting the number of singers in the area each hour of the 10-h observation day and summing the results for the day.

The 'number of singers' was the acoustic analogy of the visual count of number of individuals passing through per 10h. Singing was considered to be from the same whale if the song was heard continuously with only short gaps of a few minutes between song cycles, and no significant change in source position occurred. Where the gap was longer, we assumed that it was from the same whale if the position of the new song-session was close to that of the original song-session, if the song contained idiosyncrasies of pattern consistent with the original singer, or if the singer was tracked visually between singing locations. This method provided a direct measurement of the true number of individuals singing as they passed through the sector in the 10-h observation day, but required substantial effort, since all singers had to be tracked acoustically throughout the full observation period.

The 'singer-hour index' was determined by counting the number of singers detected within the sector once per hour and summing the results for all hours of the observation day. To avoid missing a singer during the pause between song cycles, a 10min period was monitored every hour, from 5min before the hour to 5min after the hour. This method provided a relative index of singing activity related to the number of singers and the duration of singing, since an individual singer would be counted for each hour that it is audible. The purpose of measuring this index was to test its effectiveness as a relative indicator of the number of whales passing, since it was less time consuming to measure than the actual number of singers. It did not require identification of individual singers or their locations, apart from an estimate of their ranges. In this test, the range was determined using the three-hydrophone localisation method described above, but simpler

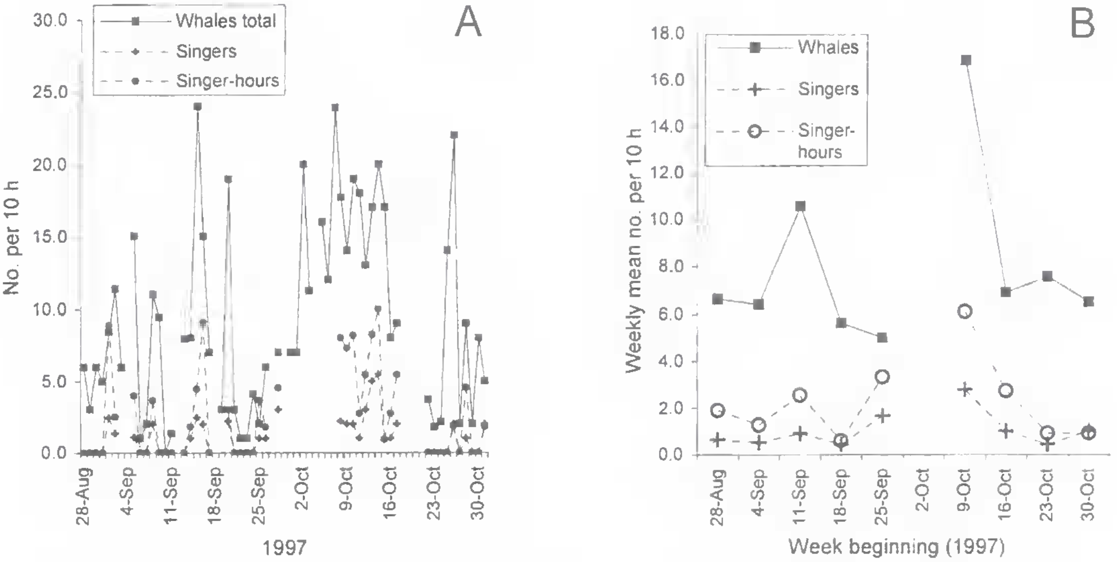

FIG. 5. Fluctuations of humpback whale visual and acoustic counts during the study period; all data averaged for 10-h sampling periods. A, daily fluctuations; B, weekly fluctuations. All visual data are shown for daily fluctuations whereas weekly averages are based only on days where both visual and acoustic data were collected. The week beginning 2 October is excluded as there were only 5 h of acoustic observations during this period.

methods of estimating range are possible. For example, if the source level of the sounds and the propagation conditions for the site are known, the range can be estimated from the level received on one hydrophone. While this index is likely to be a less effective indicator of numbers of whales passing than the number of singers, it can be measured with a simpler system and with less effort and so may be suitable for use in automated systems.

ESTIMATE OF POPULATION PARAMETERS. Four parameters of the population were estimated for the period of observation: (i) total number of south-bound whales passing through the study area, based on visual observations, (ii) total number of whales passing through the study area regardless of migratory direction, based on visual observations, (iii) total number of singers passing through the study area, based on acoustic observations, and (iv) total number of singer-hours generated in the study area. Ratios of singers and singer-hours with whales seen, across the entire study period, were calculated using these estimates.

Data for each day with 5 or more hours of observation were normalised to the equivalent for a 10-h day which was considered to be a sample unit (days with less than 5h of observation were not included in the analysis). It was assumed that the numbers of humpback whales passing Peregian Beach were unaffected by whether it was day or night, and that the numbers passing day by day varied in a random manner, apart from the broad rise and fall over the full period of migration of several months. Then our sampling could be considered to be a reasonable approximation of random sampling (Cochran, 1963). Each sample was drawn out of a population of 156 10-h units over the 65 days of observation (65 × 24/10 = 156).

Because of the long term rise and fall in numbers during migration (Fig. 5A,B), there are advantages in using stratified random sampling theory (Cochran, 1963). Application of this technique to surveys of this humpback whale population is discussed in Paterson et al. (1994, 2001). The following three strata were used for all estimates of acoustic and visual data: 28 August – 1 October (days 1-35), 2 October – 15 October (days 36-49), 16 October – 31 October (days 50-65).

A total of 55 visual sample units and 46 acoustic sample units were obtained out of a possible 156 units over the 65 day observation period. This includes acoustic data only for those days that had corresponding visual data (i.e. >5h of visual observations). Nine of the days of visual observations did not have acoustic positions because the array was down (including a scheduled maintenance period from 30 September to 8 October).

The population size with 95% confidence interval is (Cochran, 1963)

$$N\bar{y}_{st} \pm tNs(\bar{y}_{st})$$

where N is the total number of units, $\bar{y}_{st}$ is the weighted mean, t is the value of the Student's t distribution for a two-tailed value of 0.05, and $s(\bar{y}_{st})$ is the weighted estimate of standard deviation. The value of t was determined for the effective numbers of degrees of freedom (for small sample sizes, Cochran, 1963, based on Satterthwaite, 1946)

$$n_e = \frac{(\Sigma g_h s_h^2)^2}{\Sigma\left(\dfrac{g_h^2 s_h^4}{n_h - 1}\right)}$$

where n_h is the number of samples for stratum h, and s^2_h the variance of the samples in each stratum. The final term g_h is given by

$$g_h = \frac{N_h(N_h - n_h)}{n_h}$$

where N_h is the total possible number of sample units in each stratum.

Daily and weekly numbers of singers and singer-hours were correlated against each other to test the strength and significance of song activity as an indicator of the number of singers using linear regression analysis (Excel, Microsoft). Singer numbers and singer-hours were also correlated with numbers of whales seen. In addition to using population estimates to calculate ratios of song activity and whales seen across the entire study period, linear regression analysis was used to calculate regression coefficients with confidence limits for daily and weekly data.

RESULTS

VISUAL CENSUS. During the 65 day survey period, 529 hours of observations were made including 39 full 10-h days, 16 days with 5-10h, 5 days with some observations but <5h, and 5 days with no observations. A total of 279 pods of whales were observed travelling in both directions containing 501 whales including 43 calves (Fig. 6). Pods were tracked with 1,792 theodolite-measured positions. For pods with clear migratory direction, mean pod sizes were 1.73 north-bound (s.d. = 0.69, n = 52) and 1.97 south-bound (s.d. = 0.83, n = 172).

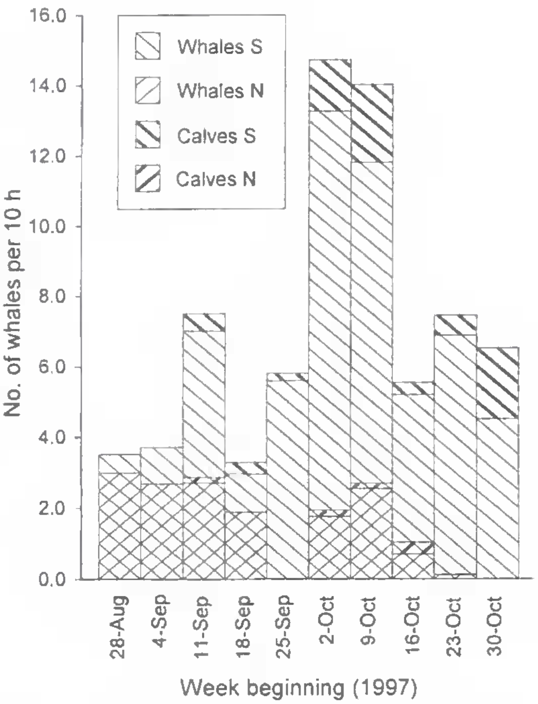

FIG. 6. Weekly numbers of visually observed humpback whales passing within 10km of Peregian Beach. Includes all visual data regardless of whether it is matched by acoustic data.

The number of south-bound whales passing within 10km of Peregian Beach between 28 August and 31 October 1997 was calculated to be 1,148 ± 170 (95% confidence interval, using techniques described by Cochran, 1963). This can be expected to significantly underestimate the stock size since: we have sampled only part of the southward migration; a significant proportion of whales passes beyond 10km at Peregian Beach; and, an unknown proportion may have been missed. An estimate of total stock passing during our limited period of observation can be made with reference to the data of Paterson et al. (1994: fig. 4) for 1992 off Point Lookout. These data show that the number of south-bound humpback whales seen passing Point Lookout between 28 August and 31 October (the period of our observations) amount to ~78% of those seen north-bound between 5 June and 31 October, the period over which their population estimate of 1,900 was made. At the annual rate of increase determined by Paterson et al. (11.7%), the population in the northern migration of 1997 is estimated to be 3,300, so that the numbers passing between 28 August and 31 October would be 2,580. Thus, if the ratio is similar off Peregian Beach, we would expect 2,580 whales to pass during our period of observation, 2.25 times the number estimated from our observations. Our estimate is therefore 45% of the numbers expected from the data of Paterson et al. The most likely explanation for this discrepancy is that approximately half the whales passed beyond the 10-km limit of the survey.

The estimated number of whales (regardless of migratory direction) passing through the study area between 28 August and 31 October 1997 was 1,424 ± 186 (95% confidence interval).

ACOUSTIC SURVEY. The full array was operational for 44 full-days, 7 part-days and not operational on 14 days due to the loss of one or more hydrophones. At least one hydrophone was operational for all but 48 hours of the survey period. Approximately 380 hours of recordings were made during the observation period although some of these were made out of visual survey hours including at night. Four hundred and thirty-two hours of array monitoring coincided with visual observations yielding 124h of recordings from an estimated 48 singers that passed within 10km of the array.

Concurrent acoustic and visual observations occurred across the survey period except for the week starting 2 October when the array was undergoing maintenance. During this week only 5h of concurrent observations were made and so analyses using average weekly data exclude this period.

The accuracy of determining the range of the source decreased with distance, small errors in determining the bearings from each pair of buoys resulting in progressively larger errors in range as range increased. Calibration results indicated that acoustic positions suffered mean range errors increasing from approximately 5% of range at 2km to 10% at 10km and 18% at 20km. These errors were for single positions using a single cue. When positions were calculated for singers, however, impossible positions based on the course and speed of the singer could be discarded allowing some improvement in accuracy. These results are consistent with other studies using similar methods that have found reasonably accurate results at ranges of 4-10 times the array dimensions (Watkins & Schevill, 1972; Cummings & Holliday, 1985; Frankel et al., 1995; Clark & Ellison, 2000).

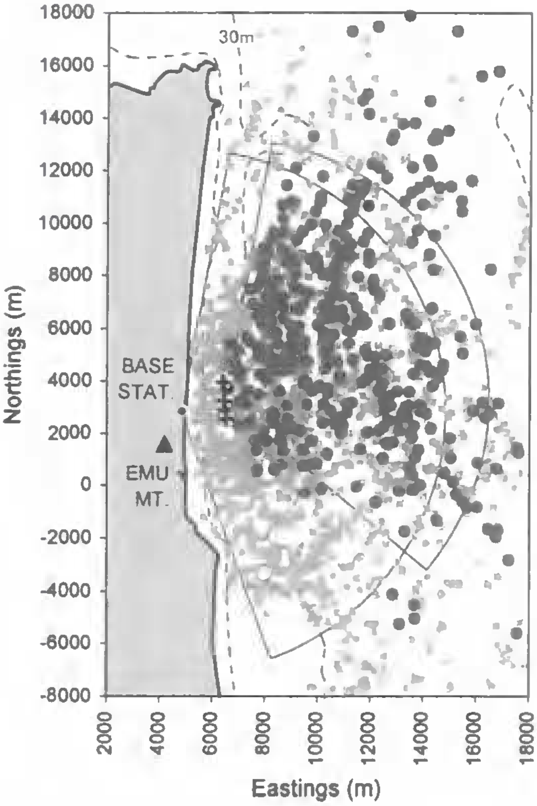

FIG. 7. Distribution of all visual (grey square) and acoustic (black dot) positions from the study. Singers could not be tracked through the southern portion of the study area due to severe attenuation of song sounds received at the array. Although whales were seen traversing the study area in less than 10m of water, singers were not recorded singing in waters of <20m depth.

Empirical observations and calibration studies showed that propagation of sound throughout the area was not uniform (Fig. 7). Sounds from tracked singers suffered sudden and severe attenuation when entering the southern part of the study area, particularly on the southernmost buoy, and so were not able to be tracked further and were often soon lost altogether on all hydrophones. This acoustic shadow was confirmed by the bulb-imploding calibration experiments and appeared to be due to the presence of a shoal south of the array. Another array 'blind spot' existed to the north of the array. Here the singers could be heard but range determination was prone to large errors within ~10° of the end-fire axis of the array (line through the hydrophones) due to the increased sensitivity of the estimates of bearings to small errors in the measured time-of-arrival-differences, as well as the increasingly acute angles of intersection of the hyperbolae. The arc of effective array function, therefore, extended from 10° to 130° (Fig. 2).

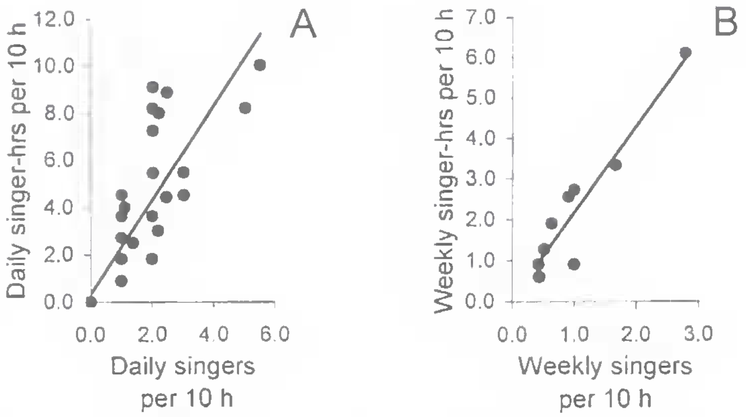

FIG. 8. Linear regression of daily and weekly numbers of singers against numbers of singer-hours of song activity. A, daily counts of singers and singer-hours normalised for a 10-h day; B, weekly averages of daily normalised counts. Only days with more than 5h of matching visual data are included.

Total singers and singer-hours in the useable portion of the study area during the study period were 180 ± 50 and 418 ± 106 (95% confidence interval) respectively. Daily and mean weekly song activity fluctuated throughout the migration in a manner that reflected the numbers of singers tracked through the study area (Fig. 8A,B). Correlation of daily singer-hours against singers gave a correlation coefficient $r = 0.86$ ($P < 0.01$, n = 44) while correlation of mean weekly singer-hours against singers gave a correlation coefficient $r = 0.94$ ($P < 0.01$, n = 9). The singer-hour index was therefore a reliable and accurate indicator of the number of singers passing through the area.

Although whales were seen traversing the study area in less than 10m of water, singers were not recorded singing in waters of <20m depth (the depth at the array) (Fig. 7).

COMPARISON OF VISUAL AND ACOUSTIC RESULTS. Numbers of singers and singer-hours also fluctuated throughout the migration in a manner similar to the numbers of whales seen (Fig. 5A,B). Correlation analysis for daily averages gave correlation coefficients $r = 0.68$ and 0.64 for singers and singer-hours, respectively ($P < 0.01$, n = 46), and for weekly averages 0.79 and 0.89, respectively ($P < 0.01$, n = 10).

Ratios of singers and singer-hours to whales seen for daily and weekly averages were determined by linear regression analysis (Fig. 9A-D, Table 1). In all cases, regression coefficients were calculated for both regression lines of best-fit and for regression lines passing through the origin (as there should have been no singers or song if there were no whales). Ratios of singers and singer-hours to whales seen were also calculated using the calculated full-survey population parameters (Table 1).

These results effectively give a range of ratios calculated from data averaged over three time frames — daily, weekly, and the entire 65-day study period. Daily results, with their greater spread and sample size, probably provide the most accurate measure of the relationships between acoustic activity and whales seen, reflected in their narrower confidence intervals. Also daily coefficients of regression are less affected by regression through the origin than

TABLE 1. Ratios and regression coefficients (*b*) with 95% confidence intervals of numbers of singers tracked and numbers of singer-hours to numbers of whales seen over three different time scales. No confidence intervals were calculated for the full survey ratios.

	Regression of daily results				Regression of weekly mean results				Full survey ratio
	Best-fit		Through origin		Best-fit		Through origin		
	b	95% CI	*b*	95% CI	*b*	95% CI	*b*	95% CI	
No. of singers vs no. of whales seen	0.137	± 0.045	0.127	± 0.027	0.138	± 0.087	0.131	± 0.035	0.126
No. of singer-hours vs no. of whales seen	0.299	± 0.110	0.288	± 0.065	0.467	± 0.199	0.345	± 0.093	0.294

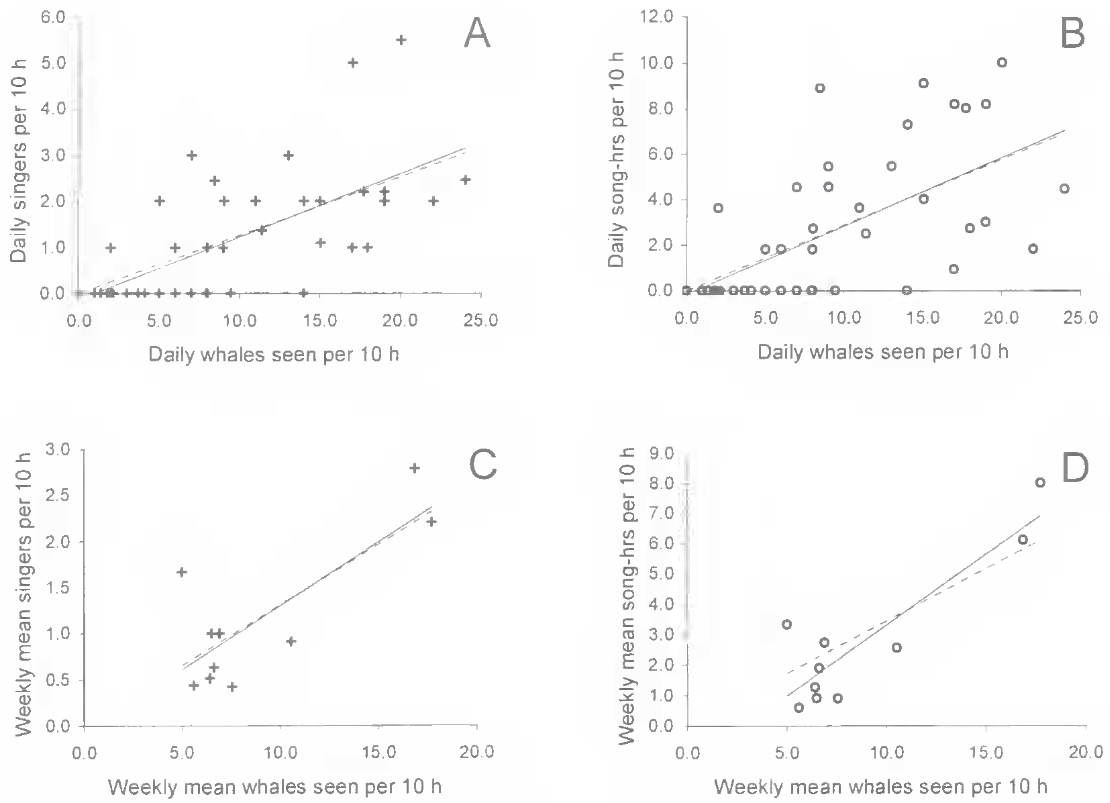

FIG. 9. Linear regression of daily and weekly numbers of whales seen against numbers of singers and singer-hours heard; solid lines are regression lines of best fit, dotted lines pass through the origin. A, daily singers and whales; B, daily singer-hours and whales; C, weekly singers and whales; D, weekly singer-hours and whales. All counts have been normalised to a 10h day. All figures are based on days with both visual and acoustic data.

weekly ones, particularly in terms of confidence limits, further suggesting their suitability as the best model used.

Although confidence limits were not calculated for population parameter-based ratios, the population parameter confidence limits suggest that they would be greater than those from the linear regression models. Unlike data used in the regression analyses, the population parameters calculated also include visual data not paired with acoustic data as the primary aim was to generate population parameters rather than ratios. Despite these differences in methodologies, the results of all analyses are in broad agreement, indicating a ratio of singers to whales of approximately 0.13 and singer-hours to whales of approximately 0.30 (Table 1).

Measures of the number of singers and total number of whales are effectively counts of the numbers of individuals passing the observation point. The results should be largely independent of the size of the observation sectors so long as there is a high probability of an individual being detected when passing through the sectors. This was the case, since whales tended to move through the full arc of the sectors, allowing individuals to be detected a number of times, both visually and acoustically. Hence, the fact that the area of the visual survey was about 25% larger than that of the acoustic survey is not expected to have significantly affected the comparison of the number of singers passing with the total number of whales passing.

On the other hand, estimates of singer-hours are likely to be proportional to the area of observation, since the index depends on the number of singers in the area at the time of measurement, and this would be proportional to the area if the density of singers were uniform or random. Hence this is a hybrid index depending on both numbers of whales passing and area of observation. The relationship between number of whales passing and the singer-hour index would need to be determined for the particular set of conditions of observation and is not applicable generally. In this study, increasing the ratio of singer-hours to whales seen by 25% would be one way to compensate for the mismatch in the visual and acoustic availability of whales.

DISCUSSION

The acoustic and visual surveys were made in a region where many passing whales could be expected to be seen within the 10km range selected. The good correlations between number of singers, the level of singing activity, and the numbers of whales seen show that acoustics can provide an effective index of relative abundance and an estimate of absolute abundance. Relationships between the number of singers and the total number of whales and between singer-hours and the number of whales are likely to vary with time of year and location and, particularly in the case of the singer-hour index, with the conditions of observation. Thus factors relating acoustic observations to abundance estimates are not universally applicable and will need to be determined for the particular time, place and conditions of observation (although, to some extent, this is also required in relating visual observations to abundance). Estimates of relative abundance would not require these factors to be determined if it is reasonable to expect them to be constant over the period of study. For example, a rate of increase over a number of years could be determined directly from the acoustic index if the observations were made at the same location and at the same time of year.

The factor relating the number of singers to the abundance depends on the proportion of whales singing, however this may vary with changes in behaviour through the breeding season and with variations in the proportion of mature males. Cato et al. (2001) found that the proportion of whales singing off the Australian east coast during the northward migration was less than half that of the southward migration, and there is evidence of variation in the amount of singing between night and day although whether this is due to more whales singing or individuals singing for longer periods is unknown (Au et al., 2000). With regards to the proportion of mature males, the east Australian population has a high rate of increase (Bryden, 1985; Paterson & Paterson, 1989; Bryden et al., 1990, 1996; Paterson et al., 1994, 2001) and so is expected to contain relatively few mature males (Best, 1993), although this may be offset to some extent by the apparent sex-bias towards males in the migratory population (Brown et al., 1995). The proportion of mature males in the population also varies during each migration due to some stratification within the migratory stream of different age, sex and reproductive classes (Chittleborough, 1965; Dawbin, 1966, 1997). The proportion of whales singing may also be different in open ocean migration to that near shore. Determination of the proportion singing over a wide range of conditions is necessary and may allow this method to be widely used.

The measure of singer-hours is less robust, since it depends also on the duration of singing and transit time of individuals, and the area of observation. In this study we have used an estimate of singer-hours based on 10min samples hourly during daylight hours as the basis of such an index, but other sampling regimes are possible and may be preferred depending on the circumstances and resources of the study. In any case, it will need to be determined for the particular set of conditions for each study. The advantage of such an index, however, is that it requires significantly less observation and analysis effort than determining the number of singers. More effort is required to 'calibrate' an index for the particular conditions, but this may be more than compensated by the substantially larger data sets that can be analysed.

Any estimate of abundance requires a determination of the spatial or temporal density of animals so that the result can be extrapolated to their full spatial or temporal range. In this study, positions of singers were determined using the time of arrival differences on the three accurately positioned hydrophones, to limit the estimate to those singers within the sector. This required substantial effort and simpler methods could be used to estimate the singer-hour index (or other song activity index), since this does not require actual location of the sources, only that they are within a chosen distance of the hydrophones. For example, distances of sources from a single hydrophone can be estimated from the received levels of the sounds if the source levels and propagation conditions are known. Propagation characteristics vary widely with location and time, however, and source levels may also vary. The results would have a larger uncertainty than those obtained by localisation, but need only a single hydrophone system and much less analysis and would be particularly suitable for automated systems or deployed packages where periodic sampling was used. Cato (1998) discusses the use of two hydrophones to determine ranges of underwater biological sound sources. In this case, the positions of the hydrophones did not need to be known and was more accurate than a single hydrophone, but still required a knowledge of propagation loss to minimise errors. The use of towed arrays in ship-based surveys may also allow positioning of whales with ambiguity, though range of detection would be less than that of fixed systems due to higher system noise (e.g. Gillespie, 1997; Clark & Fristrup, 1997). It should be noted that an estimate based on the number of singers audible without determining their distances would be quite unreliable, because of the wide range of audibility due to the large variation in ocean background noise that is expected.

This study demonstrates the importance of the effect of the acoustics of the environment, particularly in shallow water, in acoustic surveying. A shoal caused an acoustic shadow to the south and limited that area over which whales could be tracked (Fig. 7). The use of the singers themselves as a calibration tool is also demonstrated — the song could be heard to attenuate rapidly as they were followed acoustically and visually into this area.

The distribution of whale numbers over the period of the visual survey resembles closely those of previous southward migration surveys off southeast Queensland (Chittleborough, 1965; Paterson et al., 1994) demonstrating that the pattern of southward migration within 10km of Peregian Beach is representative of the migration. The results indicate, however, that a substantially larger proportion of whales pass beyond 10km of land than off Point Lookout on North Stradbroke I. The total number of humpback whales seen within 10km was about half the number that would be expected off Point Lookout between the same dates. We saw many whales beyond 10km whereas aerial surveys have shown that only 5% of whales pass Point Lookout beyond 10km (Bryden, 1985). Humpback whale migration paths would be expected to converge around Point Lookout, since this is the most easterly point in the region (Fig. 1). The effect would be a concentration of whales closer to Point Lookout than to the mainland to the north or south (Bryden, 1985; Paterson, 1991). Peregian Beach is ~100km north of Point Lookout and ~45km west, so that a greater dispersal of whales from shore might be expected there.

This greater spread of humpback whales also suggests that within the 10km limit of this study, a greater proportion pass further out than at Point Lookout. While Bryden et al. (1996) concluded that around 10-14% of pods were missed during northward migrations at Point Lookout, Findlay & Best (1996a) found that, at ranges of 6-10km, 40-50% of pods were missed at Cape Vidal, South Africa. The offshore distribution of whales at Peregian Beach may therefore lead to a higher proportion of missed whales than from Point Lookout, especially since a significant proportion may be new-born calves (about 10% of humpback whales observed off Point Lookout in the southward migration: Paterson & Paterson, 1989; Paterson et al., 1994). This survey does not attempt to correct for whales missed within 10km, but these results suggest that part of the difference with that expected from the Point Lookout surveys is due to a greater proportion of whales missed between 6-10km. However, it seems likely that most of the difference is due to the greater proportion of passing whales passing >10km off Peregian Beach.

The site of this study was chosen to be an area where visual observation is particularly effective, to provide 'ground-truthing' of acoustic methods of surveying. While this study demonstrates that acoustic methods could be effective as stand-alone surveys, it is unlikely that acoustic surveys will be conducted in preference to land-based visual surveys where these are possible. The main application of acoustic surveys would be to regions where visual surveying is limited, such as the open ocean, where acoustic systems could be left to record for months at a time. Acoustics may also be useful in conjunction with visual surveying by providing a second, independent method of counting whales to improve the reliability of observations.

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LITERATURE CITED

AU, W.W.L., MOBLEY, J., BURGESS, W.C., LAMMERS, M.O. & NACHTIGALL, P.E. 2000. Seasonal and diurnal trends of chorusing humpback whales wintering in waters off western Maui. Marine Mammal Science 16(3): 530-544.

BAKER, C.S. & HERMAN, L.M. 1987. Alternative population estimates of humpback whales (*Megaptera novaeangliae*) in Hawaiian waters. Canadian Journal of Zoology 65: 2818-2821.

BAKER, C.S., HERMAN, L.M. & PERRY, A. 1985. Population characteristics and migration of summer and late-season humpback whales (*Megaptera novaeangliae*) in southeastern Alaska. Marine Mammal Science 1(4): 304-323.

BANNISTER, J.L. 1985. Southern right (*Eubalaena australis*) and humpback (*Megaptera novaeangliae*) whales off Western Australia: some recent work. Pp. 105-114. In Ling, J.R. & Bryden, M.M. (eds) Studies of sea mammals in south latitudes. (South Australian Museum: Adelaide).

BANNISTER, J.L., KIRKWOOD, G.P. & WAYTE, S.E. 1991. Increase in humpback whales off Western Australia. Report of the International Whaling Commission 41: 461-465.

BEST, P.B. 1993. Increase rates in severely depleted stocks of baleen whales. ICES Journal of Marine Science 50: 169-186.

BROWN, M.R., CORKERON, P.J., HALE, P.T., SCHULTZ, K.W. & BRYDEN, M.M. 1995. Evidence for a sex-segregated migration in the humpback whale (*Megaptera novaeangliae*). Proceedings of the Royal Scoiety of London; Series B 259: 229-234.

BRYDEN, M.M. 1985. Studies of humpback whales (*Megaptera novaeangliae*), Area V. Pp. 115-123. In Ling, J.R. & Bryden, M.M. (eds) Studies of sea mammals in south latitudes. (South Australian Museum: Adelaide).

BRYDEN, M.M. & SLADE, R.W. 1988. Survey of humpback whales (*Megaptera novaeangliae*) off eastern Australia, 1987. Report for the Australian National Parks and Wildlife Service. (Department of Veterinary Anatomy, University of Sydney: Sydney).

BRYDEN, M.M., BROWN, M.R., FIELD, M.S., CLARKE, E.D. & BUTTERWORTH, D.S. 1996. Survey of humpback whales (*Megaptera novaeangliae*) off eastern Australia, 1996. Report to the Australian Nature Conservation Agency (Department of Veterinary Anatomy, University of Sydney: Sydney).

BRYDEN, M.M., KIRKWOOD, G.P. & SLADE, R.W. 1990. Humpback whales, Area V. An increase in numbers off Australia's east coast. Pp. 271-277. In Kelly, K.R. & Hempel, G. (eds) Antarctic ecosystems: ecological change and conservation (Springer-Verlag: Berlin).

BUCKLAND, J.L., ANDERSON, D.R., BURNHAM, K.P. & LAAKE, J.L. 1993. Distance sampling: estimating abundance of biological populations. (Chapman & Hall: New York).

CATO, D.H. 1984. Recording humpback whale sounds off Stradbroke Island. Pp. 285-290. In Coleman, R.J., Covacevich, J. & Davie, P. (eds) Focus on Stradbroke. (Boolarong Publications: Brisbane).

1991. Songs of humpback whales: the Australian perspective. Memoirs of the Queensland Museum 30(2): 277-290.

1998. Simple methods of estimating source levels and locations of marine animal sounds. Journal of the Acoustical Society of America 104(3): 1667-1678.

CATO, D.H., PATERSON, R. & PATERSON, P. 2001. Vocalisation rates of migrating humpback whales over 14 years. Memoirs of the Queensland Museum 47(2): 481-489.

CHITTLEBOROUGH, R.G. 1965. Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). Australian Journal of Marine and Freshwater Research 16: 33-128.

CLAPHAM, P.J. & MATTILA, D.K. 1990. Humpback whale songs as indicators of migration routes. Marine Mammal Sciemce 6(2): 155-160.

CLARK, C.W. & ELLISON, W.T. 1989. Numbers and distributions of bowhead whales, *Balaena mysticetus*, based on the 1986 acoustic study off Pt. Barrow, Alaska. Report of the International Whaling Commission 39: 297-303.

2000. Calibration and comparison of the acoustic location methods used during the spring migration of the bowhead whale, *Balaena mysticetus*, off Pt. Barrow, Alaska, 1984-1993. Journal of the Acoustical Society of America 107(6): 3509-3517.

CLARK, C.W. & FRISTRUP, K.M. 1997. Whales '95: A combined visual and acoustic survey of blue and fin whales off southern California. Report of the International Whaling Commission 47: 583-600.

CLARK, C.W., CHARIF, R., MITCHELL, S. & COLBY, J. 1996. Distribution and behavior of the Bowhead whale, *Balaena mysticetus*, based on the analysis of acoustic data collected during the 1993 spring migration off Point Barrow, Alaska. Report of the International Whaling Commission 46: 541-552.

CLARK, C.W., ELLISON, W.T. & BEEMAN, K. 1986. A preliminary account of the acoustic study conducted during the 1985 spring bowhead whale, *Balaena mysticetus*, migration off Point Barrow, Alaska. Report of the International Whaling Commission 36: 311-316.

COCHRAN, G.C. 1963. Sampling Techniques. 2nd edn. (Wiley: New York).

CORKERON, P.J., BROWN, M., SLADE, R.W. & BRYDEN, M.M. 1994. Humpback whales, *Megaptera novaeangliae* (Cetaeca: Balaenopteridae), in Hervey Bay, Queensland. Wildlife Research 21: 293-305.

CUMMINGS, W.C. & HOLLIDAY, D.V. 1985. Passive acoustic location of bowhead whales in a population census off Point Barrow, Alaska. Journal of the Acoustical Society of America 78(4): 1163-1169.

DARLING, J.D. & MORI, K. 1993. Recent observations of humpback whales (*Megaptera novaeangliae*) in Japanese waters off Ogasawara and Okinawa. Canadian Journal of Zoology 71: 325-333.

DARLING, J.D. & MOROWITZ, H. 1986. Census of 'Hawaiian' humpback whales (*Megaptera novaeangliae*) by individual identification. Canadian Journal of Zoology 64: 105-111.

DAWBIN, W.H. 1966. The seasonal migratory cycle of Humpback whales. Pp. 145-170. In Norris, K.S. (ed) Whales, dolphins and porpoises. (University of California Press: Berkeley).

1997. Temporal segregation of humpback whales during migration in southern hemisphere waters. Memoirs of the Queensland Museum 42(1): 105-138.

DAWBIN, W.H. & GILL, P.C. 1991. Humpback whale survey along the west coast of Australia: A comparison of visual and acoustic observations. Memoirs of the Queensland Museum 30(2): 255-257.

FINDLAY, K.P. & BEST, P.B. 1996a. Assessment of heterogeneity in sighting probabilities of humpback whales within viewing range of Cape Vidal, South Africa. Marine Mammal Science 12(3): 335-353.

1996b. Estimates of the numbers of humpback whales observed migrating past Cape Vidal, South Africa, 1988-1991. Marine Mammal Science 12(3): 354-370.

FLÓREZ-GONZÁLEZ, L. 1991. Humpback whales *Megaptera novaeangliae* in the Gorgona Island, Colombian Pacific breeding waters: population and pod characteristics. Memoirs of the Queensland Museum 30(2): 291-295.

FRANKEL, A.S., CLARK, C.W., HERMAN, L.M. & GABRIELE, C.M. 1995. Spatial distribution, habitat utilization, and social interactions of humpback whales, *Megaptera novaeangliae*, off Hawaii, determined using acoustic and visual techniques. Canadian Journal of Zoology 73: 1134-1146.

FRISTRUP, K.M. & CLARK, C.W. 1997. Combining visual and acoustic survey data to enhance density estimation. Report of the International Whaling Commission 47: 933-936.

GENTLEMAN, R. & ZEH, J.E. 1987. A statistical model for estimating the number of bowhead whales, *Balaena mysticetus*, passing a census point from combined visual and acoustic data. Report of the International Whaling Commission 37: 313-327.

GILL, P.C., EYRE, E.J., GARIGUE, C. & DAWBIN, W.H. 1995. Observations of humpback whales (*Megaptera novaeangliae*) on a cruise to New Caledonia and the Chesterfield Reefs. Memoirs of the Queensland Museum 38(2): 505-511.

GILLESPIE, D. 1997. An acoustic survey for sperm whales in the Southern Ocean sanctuary conducted from the RSV Aurora Australis. Report of the International Whaling Commission 47: 897-907.

HERMAN, L.M. & ANTINOJA, R.C., 1977. Humpback whales in the Hawaiian breeding waters: Population and pod characteristics. Scientific Reports of the Whale Research Institute 29: 59-85.

INGHAM, A.E. 1975. Sea surveying. (John Wiley & Sons: London).

KIBBLEWHITE, A.C., DENHAM, R.M. & BARNES, D.J., 1967. Unusual low-frequency signals observed in New Zealand waters. Journal of the Acoustical Society of America 41: 644-655.

LEVENSON, C. & LEAPLEY, W.T., 1978. Distribution of humpback whales (*Megaptera novaeangliae*) in the Caribbean determined by a rapid acoustic method. Journal of the Fisheries Research Board Canada 35: 1150-1152.

MACKNIGHT, F.L., CATO, D.H., NOAD, M.J. & GRIGG, G.C. 2001. Qualitative and quantitative analysis of the song of the east Australian population of humpback whales. Memoirs of the Queensland Museum 47(2): 525-537.

MATTILA, D.K. & CLAPHAM, P.J. 1989. Humpback whales, *Megaptera novaeangliae*, and other cetaceans on Virgin Bank and in the northern Leeward Islands, 1985 and 1986. Canadian Journal of Zoology 67: 2201-2211.

MATTILA, D.K., CLAPHAM, P.J., VÁSQUEZ, O. & BOWMAN, R.S. 1994. Occurrence, population composition, and habitat use of humpback whales in Samana Bay, Dominican Republic. Canadian Journal of Zoology 72(11): 1898-1907.

McDONALD, M.A. & FOX, C.G. 1999. Passive acoustic methods applied to fin whale population density estimation. Journal of the Acoustical Society of America 105(5): 2643-2651.

NOAD, M.J., CATO, D.H., BRYDEN, M.M., JENNER, M-N. & JENNER, K.C.S. 2000. Cultural revolution in whale songs. Nature 408: 537.

NORRIS, T.F., McDONALD, M. & BARLOW, J. 1999. Acoustic detections of singing humpback whales (*Megaptera novaeangliae*) in the eastern North Pacific during their northbound migration. Journal of the Acoustical Society of America 106(1): 506-514.

PATERSON, R. 1984. Migration patterns of humpback whales (*Megaptera novaeangliae*) in the waters adjacent to Moreton and North Stradbroke Islands. Pp. 342-347. In Coleman, R.J., Covacevich, J. & Davie, P. (eds) Focus on Stradbroke. (Boolarong Publications: Brisbane).

1991. The migration of humpback whales *Megaptera novaeangliae* in east Australian waters. Memoirs of the Queensland Museum 30(2): 333-341.

PATERSON, R. & PATERSON, P. 1984. A study of the past and present status of humpback whales in east Australian waters. Biological Conservation 29: 321-343.

1989. The status of the recovering stock of humpback whales *Megaptera novaeangliae* in east Australian waters. Biological Conservation 47: 33-48.

PATERSON, R., PATERSON, P. & CATO, D.H. 1994. The status of humpback whales *Megaptera novaeangliae* in east Australia thirty years after whaling. Biological Conservation 70: 135-142.

2001. The status of humpback whales in east Australia at the end of the 20th Century. Memoirs of the Queensland Museum 47(2): 579-586.

PAYNE, R.S. & McVAY, S. 1971. Songs of humpback whales. Science 173: 585-597.

RAFTERY, A.E. & ZEH, J.E. 1998. Estimating bowhead whale population size and rate of increase from the 1993 census. Journal of the American Statistical Association 93: 451-463.

RAFTERY, A.E., ZEH, J.E., YANG, Q. & STYER, P.E. 1990. Bayes empirical Bayes interval estimation of bowhead whale, *Balaena mysticetus*, population size based on the 1986 combined visual and acoustic census at Point Barrow, Alaska. Report of the International Whaling Commission 40: 393-409.

SMITH, T.D., ALLEN, J., CLAPHAM, P.J., HAMMOND, P.S., KATONA, S., LARSEN, F., LIEN, J., MATTILA, D., PALSBØLL, P.J., SIGURJÓNSSON, J., STEVICK, P.T. & ØIEN, N. 1999. An ocean-basin-wide mark-recapture study of the North Atlantic humpback whale (*Megaptera novaeangliae*). Marine Mammal Science 15(1): 1-32.

STONE, G.S. & HAMNER, W.M. 1988. Humpback whales *Megaptera novaeangliae* and southern right whales *Eubalaena australis* in Gerlache Strait, Antarctica. Polar Record 24(148): 15-20.

THOMAS, J.A., FISHER, S.R., FERM, L.M. & HOLT, R.S. 1986. Acoustic detection of cetaceans using a towed array of hydrophones. Report of the International Whaling Commission (Special Issue 8): 139-148.

WATKINS, W.A. & SCHEVILL, W.E. 1972. Sound source location by arrival-times on a non-rigid three-dimensional hydrophone array. Deep Sea Research 19: 691-708.

WHITEHEAD, H. 1982. Populations of humpback whales in the northwest Atlantic. Report of the International Whaling Commission 32: 345-353.

WINN, H.E. & WINN, L.K. 1978. The song of the humpback whale (*Megaptera novaeangliae*) in the West Indies. Marine Biology 47: 97-114.

WINN, H.E., EDEL, R.K. & TARUSKI, A.G. 1975. Population estimate of the humpback whale (*Megaptera novaeangliae*) in the West Indies by visual and acoustic techniques. Journal of the Fisheries Research Board Canada 32(4): 499-506.

WÜRSIG & CLARK, C. 1993. Behavior. Pp. 157-199. In Burns, J.J., Montague, J.J. & Cowles, C.J. (eds) The bowhead whale book. (Society for Marine Mammalogy: Lawrence, KS).

ZEH, J.E., CLARK, C.W., GEORGE, J.C., WITHROW, D., CARROLL, G.M. & KOSKI, W.R. 1993. Current population size and dynamics. Pp. 409-489. In Burns, J.J., Montague, J.J. & Cowles, C.J. (eds) The bowhead whale book. (Society for Marine Mammalogy: Lawrence, KS).

APPENDIX

DETERMINATION OF THE RANGE TO A WHALE USING THEODOLITE ANGLES

This study uses a technique derived from basic trigonometry to calculate the distance of a whale from the observation point, allowing for the curvature of the earth and refraction.

The angular effect of refraction is expressed as a *coefficient of refraction*, k, the ratio of the difference between the true and apparent angles to the whale, r, and the angle subtended at the centre of the earth, θ , ie. $k = r/\theta$. The value of k over water is generally accepted as being 0.08 (Ingham, 1975) and the appropriateness of this value was confirmed empirically during our calibration experiments. As k is theoretically applicable to the correct angle θ, an iterative process is required where, for each iteration, a correction to the apparent angle α is calculated based on the previous iteration's θ. A series of six iterations was sufficient to calculate a true value of α to less than one second of arc, exceeding the limitations of the theodolites used.

In Appendix Fig. 1, R = radius of the earth (6,372km at 27°S), H = height of theodolite above sea level, D = distance along the surface of the sea from the base of the observation point to the whale, and α = the azimuth (vertical angle to the object). Since in any triangle the ratios of the sines of the internal angles to the lengths of the opposite sides are equal,

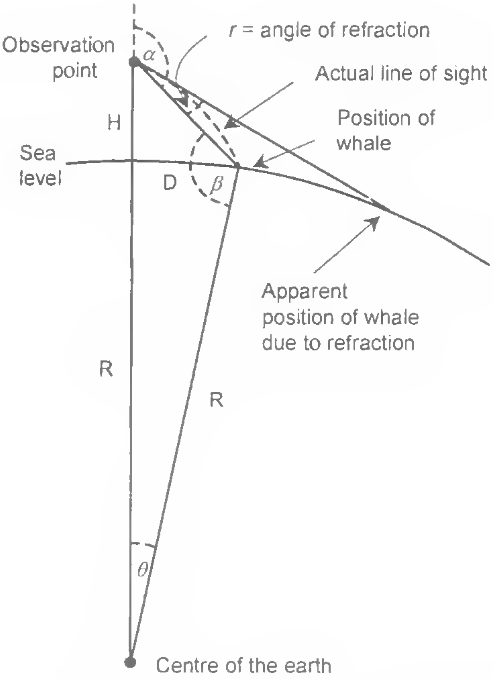
$$\frac{\sin\alpha'}{R} = \frac{\sin\beta}{R+H} \qquad \text{where } \alpha' = 180 - \alpha$$

$$\text{so that} \quad \beta' = \sin^{-1}\left(\frac{\sin\alpha\,(R+H)}{R}\right) \qquad \text{where } \beta' = 180 - \beta$$

$$\text{Now} \quad \theta = 180 - \alpha' - \beta$$
$$= \alpha + \beta' - 180$$

Therefore

$$D = R\theta\frac{\pi}{180} = \frac{R\pi}{180}\left(\alpha + \sin^{-1}\left(\frac{\sin\alpha(R+H)}{R}\right) - 180\right)$$



APPENDIX FIG. 1. Geometry of the use of a land-based theodolite to measure the range of objects at sea.